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WOODPECKER BILLS AND THEIR CONFORMANCE TO HUTCHINSONIAN RATIOS[1]

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ABSTRACT. Culmen lengths of a bark-drilling guild were examined to evaluate the utility of Hutchinsonian ratios. The culmen lengths of species pairs which feed on relatively abundant intermediate size prey were nearly identical. Species pairs which fed on the relatively less abundant very small and very large prey species had large (1.35-1.47) culmen ratios. It is concluded that Hutchinsonian ratios may, if used with discretion, serve as useful indicators of potential competition but should not be assumed to be indirect evidence of competition.

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INTRODUCTION

The role of competition in structuring species assemblages long has captured the interest of ecologists (Schoener 1982) and has received increasingly critical attention (Lawton and Strong 1981, Simberloff and Boecklen 1981). Hutchinson (1959) approached the issue by asking the question of how similar organisms could be and still coexist. He offered the tentative observation that pairs of sympatric congeners exhibit ratios of body weight of about two and ratios of the linear dimensions of feeding appendages of approximately 1.3. Hutchinsonian ratios were originally applied to sympatric congeneric species pairs under the assumption that closely related species should be, at least potentially, the most intense competitors (Hutchinson 1959, Schoener 1965). Subsequent investigators have made frequent use of the Hutchinsonian ratios both between congeners (Klopfer and MacArthur 1961, Schoener 1965) and noncongeneric species (Price 1972), but serious questions have been raised concerning their validity and usefulness (Fagerstrom 1978, Roth 1981, Simberloff and Boecklen 1981).

The purpose of this study was to investigate the value of Hutchinsonian ratios in a bark-drilling guild (Root 1967) of birds in eastern North America. These guild members potentially coexist in large areas throughout the year (Bock and Lepthien 1975, Falk 1978, see range maps in Peterson 1980). By comparing Hutchinsonian ratios of guild members with the sizes of prey organisms in the birds' diet it may be possible to ascertain whether the ratios have any ecological correlates.

METHODS AND MATERIALS

Culmen lengths were measured to the nearest 0.05 mm on representative museum specimens of guild members of the eastern bark-drilling guild: downy woodpecker *(Picoides pubescens)*, yellow-bellied sapsucker *(Sphyriapicus varius)*, red-headed woodpecker *(Melanerpes erythrocephalus)*, red-bellied woodpecker *(M. carolinus)*, hairy woodpecker *(P. villosus)*, common flicker *(Colaptes auratus)* and pileated woodpecker *(Dryocopus pileatus)*. Guild members were arrayed in order of increasing size. Ratios of the culmen length were calculated between adjacent members of the guild (table 1).

Museum specimens originated in Ohio and Indiana except for eight pileateds which were from Illinois. Members of the guild are known to coexist during some portion of the year in the areas from which the museum specimens were obtained (Bock and Lepthien 1975). All specimens were in adult plumage.

Beetles were selected to represent typical prey organisms because of their common occurrence in the diets of guild members (Beal 1911). The identity of beetle species that serve as prey items for woodpeckers were obtained through the literature. Beetle prey sizes to the nearest 0.1 mm were determined through descriptions available in the entomological literature. (References used to determine woodpecker beetle prey and beetle sizes may be obtained

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TABLE 1

Mean culmen lengths and Hutchinsonian ratios in a bark-drilling guild in eastern North America. Means followed by the same letter are not significantly ($P > 0.05$) different from each other.

Species	N (♂/♀)	Mean length mm (S.D.)	Ratio
Downy woodpecker	20 (10/10)	17.9 (1.14) a	1.35
Yellow-bellied sapsucker	20 (10/10)	24.1 (0.68) b	1.18
Red-headed woodpecker	14 (9/5)	28.9 (2.51) c	1.04
Red-bellied woodpecker	19 (10/9)	29.7 (1.56) c	1.02
Hairy woodpecker	20 (10/10)	30.2 (2.05) c	1.16
Common flicker	19 (10/9)	35.0 (2.05) d	1.47
Pileated woodpecker	13 (6/7)	51.6 (4.18) e	
Hairy:Downy ratio			1.67

from the author upon request.) Beetle prey were grouped into three-mm size classes, and the relative abundance of each size class was determined.

Differences among mean beetle sizes and culmen lengths were determined with unbalanced, single factor analysis of variance with mean separation accomplished by Duncan's New Multiple Range Test (Duncan 1955).

RESULTS

Mean culmen lengths of the bark-drilling guild ranged from 17.9 mm (downy) to 51.6 mm (pileated) (table 1). There was a significant ($P < 0.001$) difference in culmen length among the guild members. Hutchinsonian ratios calculated from adjacent species pairs ranged from 1.02 to 1.47 (table 1). Species pairs, ordered by increasing size, demonstrate a pattern of large ratios occurring in those pairs at either end of the guild size distribution. Ratios approaching unity are characteristic of species pairs which are intermediate in size. Red-headed, red-bellied and hairy woodpeckers all have bill lengths of approximately 29 mm.

Beetle prey size is log-normally distributed; i.e., there is a relative abundance of small to medium size beetles utilized as food by guild members (fig. 1). Very small and large beetle species contribute less to woodpecker diets in terms of relative abundance. There was a significant ($P < 0.001$) difference among the sizes of beetles selected by the woodpeckers as their prey. In general, as woodpecker culmen lengths increased, the size of the beetles selected as prey items increased (table 2).

DISCUSSION

Fagerstrom (1978), in an admonition against the unjudicious use of Hutchinsonian ratios, stressed that the ratios should not be used as *ex post facto* evidence of character displacement believing that such ratios serve merely as reflections of branching points in phyletic evolution, or, of the magnitude of genetic-chromosomal evolution. It is unlikely that bill length ratios are accurate reflections of past evolutionary history. Warnings have been sounded concerning the use of bill shape as a systematic character at the generic level because of possible influences of past biological interactions (Bock 1964). Bill length is, however, a character which appears to be ecologically important and, consequently, appears to be morphologically labile (Lack 1968).

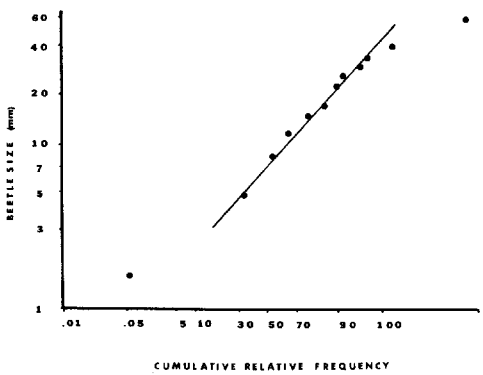

FIGURE 1. A plot of the cumulative relative frequency of the beetle size classes (three mm) plotted on a long-normal coordinate system.

TABLE 2

Mean lengths of beetle species reported in the diets of bark-drilling guild members in eastern North America. Means followed by the same letter are not significantly different from each other.

Guild member	Number of beetle species	Mean length mm (S.D.)
Downy woodpecker	35	5.6 (3.2) a
Yellow-bellied sapsucker	13	6.1 (2.7) a
Red-headed woodpecker	56	12.9 (7.5) c, d
Red-bellied woodpecker	14	13.1 (8.8) c, d
Hairy woodpecker	22	10.9 (10.1) c, d
Common flicker	31	9.1 (5.1) b, c
Pileated woodpecker	6	15.5 (8.5) d

No firm conclusions can be drawn concerning the value of Hutchinsonian ratios in the case of the bark-drilling guild examined here. Species pairs which feed on the less abundant size class of preyed-upon beetles have the largest culmen ratios (downy:sapsucker 1.35; flicker:pileated 1.47), while those which feed upon the relatively abundant size classes of beetles have ratios which are much smaller than Hutchinson's (1959) example of 1.3 (sapsucker:red-headed 1.18; red-headed:red-bellied 1.04; red-bellied:hairy 1.02; hairy:flicker 1.16) in accordance with Schoener's prediction (1965) that species with small overlap in a relevant character feed on relatively abundant food resources. It may be that the woodpeckers with intermediate size bills have little need to compete for these relatively abundant food resources.

Alternatively, species enjoying abundant food resources may have a narrower niche width allowing for the coexistence of more species along that niche dimension. Resource partitioning in the intermediate size species, if it occurs at all, may involve a different resource dimension. Indeed, there are numerous accounts of interspecific territoriality, agonistic behavior and microhabitat differences among these species (Willson 1970, Reller 1972, Moskovitz 1978). The possibility cannot be ruled out however, that the species existing at either end of the size distribution may, in part, be partitioning food resources on the basis of size.

This analysis remains speculative when restricted to beetle prey. Many of the woodpeckers feed extensively on other types of food items (Beal 1911). During the non-breeding season however, the diet of many of the woodpeckers is restricted in part to wood-boring insects such as beetles, or to wood-boring insects and stored mast (Reller 1972). Somewhat more credence is added when analysis of the plant foods of woodpeckers demonstrates a log-normal distribution (Woods unpubl. data) similar to that shown by beetles.

Clearly, the predicted 1.3 ratio is not evident in my data. The bill sizes of this species assemblage does vary with the apparent availability of beetle resource as indicated by the relative numbers of differently sized beetle species serving as prey items. It would be interesting to investigate other guilds to determine if relevant morphological characters covary with trophic resources in a similar fashion. If this pattern were to be repeated then Hutchinsonian ratios may offer potential insights into interspecific relationships. If interpreted carefully, they can serve as suggestive stimuli for further, more complete, investigations of potential competition rather than as confirmation of preconceived notions.

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